A synopsis of the South American genus *Gomphomacromia* (Odonata: Gomphomacromiinae)

Natalia von Ellenrieder¹ & Rosser W. Garrison²

¹ Aquatic Bioassessment Laboratory, 2005 Nimbus Road, Rancho Cordova, CA 95670, USA. <odo_nata@hotmail.com>
² California Department of Food and Agriculture, 3294 Meadowview Road, Sacramento, CA 95616, USA. <rwgarrison@earthlink.net>

Key words: Odonata, dragonfly, Gomphomacromiinae, Gomphomacromia, taxonomy, phylogeny, diagnostic keys, South America.

ABSTRACT

Gomphomacromia mexicana is shown to be a junior synonym of G. chilensis based on a comparison of the holotype male with the original description of G. chilensis and specimens identified as that species from Chile. Examination of a large series of specimens from central and southern Chile and Argentina identified both as G. paradoxa and G. etcheverryi shows the proposed diagnostic characters for the two taxa variable, thus G. etcheverryi is considered a junior synonym of G. paradoxa. Illustrated keys, distribution maps and a cladistic analysis for the four known species of the genus are provided.

Introduction

The genus Gomphomacromia Brauer, 1864 comprises small black and yellow anisopterans inhabiting streams and seepages along the Andean mountain range in South America. The genus shows Gondwanic affinities to the Australian Gomphomacromiinae genera (Theischinger & Watson 1978, 1984; Carle 1995). Six species names have been used recently for this genus: G. paradoxa Brauer, 1864 from southern Chile and Argentina (Jurzitza 1981; Theischinger & Watson 1984; Muzón 1995, 1997), G. etcheverryi Fraser, 1957 from central Chile and southern Argentina (Fraser 1957, 1958; Jurzitza 1981; Muzón 1995, 1997), G. chilensis Martin, 1921 from central Chile (Martin 1921; Jurzitza 1981), G. nodisticta Ris, 1928 from northern Argentina (Ris 1928; von Ellenrieder 2000), G. fallax McLachlan, 1881 from Ecuador, Peru, and Bolivia (Ris 1918, 1928; Schmidt 1942; Beckemeyer 2002), and G. mexicana Needham, 1933 from Mexico (Needham 1933).

Diagnostic characters used in the original descriptions for various species of *Gomphomacromia* have largely been based on thoracic and abdominal color patterns, and assignment of some specimens to various names has been difficult. The description of *G. mexicana* was based on a single male, lacked illustrations, and its identity has remained doubtful since no further specimen of *Gomphomacromia* has ever been collected again in Mexico (González Soriano & Novelo Gutiérrez 1996) or north of Ecuador. Examination of the type specimen against original description and specimens from Chile shows it to be a junior synonym of *G. chilensis*.

We have found it difficult to assign specimens from Chile and Argentina unambiguously to G. paradoxa or G. etcheverryi. Geographic variation in color pattern in G. paradoxa was observed by Ris (1928) who considered three of his specimens as a variety ("G. paradoxa forma"). Fraser (1957, 1958), however, considered these differences worthy of a specific name, and created a new species, G. etcheverryi, based on four specimens with more extensive yellow areas on the sides of the pterothorax, and more extensive dark areas at the wing bases (Fraser 1958), thus restricting the name G. paradoxa to specimens with lateral yellow areas divided into two discrete spots. Jurzitza (1981), finding color pattern to be unreliable, separated G. paradoxa and G. etcheverryi primarily by geographic distribution. He assigned the name G. etcheverryi to specimens ranging from Illapel (31°S, 71°W) to Temuco (38°S, 72°W) in central Chile, and restricted G. paradoxa to specimens from southern Chile and Argentina. He also provided characters from cerci morphology and ultrastructure of vesica spermalis to separate males of the two species (Jurzitza 1981). Based on an examination of over 60 specimens from the entire distributional range of G. paradoxa and G. etcheverryi in Chile and Argentina, we found no supporting evidence for the existence of two species; color and morphological characters from cerci and vesica spermalis are variable and not correlated with geography. Accordingly, we consider G. etcheverryi a junior synonym of G. paradoxa.

Here we diagnose the genus, provide synonymic lists and updated distribution maps, and include a cladistic analysis and keys for adults of all four species based on structural characters.

MATERIAL AND METHODS

Specimens examined

All specimens were examined to establish variability of characters. Characters were illustrated with the aid of a camera lucida and drawings are not to scale. Acronyms used for collections are as follows:

RWG
 R.W. Garrison personal collection, Sacramento, CA, USA
 NHMS
 Museo Nacional de Historia Natural, Santiago, Chile
 Museo Nacional de La Plata, Buenos Aires, Argentina

Gomphomacromia chilensis — Chile: Región Metropolitana de Santiago, Santiago Prov., 1 &, 1 &, Macul, 650 m, ii 1975 (RWG). — ? Mexico: 1 & [Holotype G. mexicana Needham, 1933 – No. 1127], Teotlhuacan, leg. L.H. McDaniels, 26 vii 1921 (Cornell Univ.).

G. fallax — Ecuador: Napo Pastaza Dep., 1 o, Abitagua, Río Pastaza watershed, 1,000 m, leg. W.Clarke-MacIntyre, 05 xi 1939 (RWG). — Peru: Madre De Dios Dept., 3 o, Manu, Pakitza, trail 2, 250 m, leg. O.S. Flint, Jr., 20 ix 1988 (RWG), 1 Q, Manu, "Erika", across Alto Madre de Dios from Salvación, 550 m, leg. O.S. Flint, 06 ix 1988 (RWG); 2 o, Cuzco Dept., Paucartambo Prov., Pillcopata to Atalaya, roadside seeps, 1,000 m, leg. O.S. Flint, Jr., 09 iv 1988 (RWG). — Bolivia: La Paz Dept., Nor Yungas Prov., 3 o, 2 Q, Coroico, rivulet at path to town water source, 1,890 m, leg. N. v. Ellenrieder, 13 i 2000 (MLP; RWG).

G. nodisticta — Argentina: Salta Prov., San Carlos Dept., 7 o, 2 o, San Antonio mountain stream, 1,650 m, leg. N. v. Ellenrieder, 02 iv 1999 (MLP).

G. paradoxa — Chile: Región de Coquimbo: Choapa Prov., 1 Q, Hacienda Illapel, leg. E.I. Schlinger, M. Irwin and L. Peña, 19 x 1966 (RWG); Región de Valparaíso: Aconcagua Prov., 1 &, Los Andes, 790 m, leg. C. Cook, xii 1977 (RWG); Región Metropolitana de Santiago: Santiago Prov., 3 o, Lo Canas, 700 m, leg. C. Cook, 01/30 xi 1963 (RWG); Región del Maule: Curico Prov., 1 Q, Río Teno, Cordillera de Curico, 1,300 m, leg. C. Cook, 07 ii 1965 (RWG); 2 σ , 2 ρ , same but 1,500 m, leg. C. Cook, 06 ii 1962 (RWG); Cauquenes Prov., 1 σ , 15 km E Curanipe, leg. E. Schlinger, 24 i 1967 (RWG); Región de la Araucania: Malleco Prov., 1 o, Angol, Los Ayres, 65 m, leg. D.S. Bullock, 25 vi 1945 (RWG); 1 of, Cord. Nahuelbuta, Los Gringos camp, leg. C.M. and O.S. Flint, Jr., 18 xii 1993 (RWG); Región de Los Lagos: Palena Prov., 3 &, 1 Q, Camping Arrayanes, 5 km NW Chaiten, 400 m, leg. C.M. and O.S. Flint, Jr., 20-21 i 1987 (RWG); 10, 10, Caleta Gonzalo, Parque Pumalin, leg. A. Vera, 2-9 ii 2004 (NHMS); Chiloe Prov., 10, 10, 4 km E Ahoni Alto, leg. C.M. and O.S. Flint, Jr., 24 xii 1993 (RWG); Región de Aisén: Aisén Prov., 2 o, 3 o, Puerto Aisén, marsh 5 km S Lago Riesco, leg. J. Muzón and R.W. Garrison, 20 i 1995 (MLP, RWG); 8 &, marsh areas nr. Lago Riesco, S of Puerto Aisen, leg. R.W. Garrison, 20 i 1995 (RWG); 6 of, marsh 3-4 km N of Lago Riesco, S of Puerto Aisen, leg. R.W. Garrison, 20 i 1995 (RWG); 1 Q, Termas El Chiconal, W of Puerto Aisen (by boat), leg. R.W. Garrison, 22 i 1995 (RWG); 3 of, small stream above Laguna Pedro Aguirre Cerda, by route 7, 2 km S of turnoff to Mina El Toqui, leg. R.W. Garrison, 23 i 1995 (RWG); 1 o, Parque Nacional Queulat, at route 7, 100 m S of Cuesta Norte, leg. R.W. Garrison, 25 i 1995 (RWG); 7 σ , 1 \circ , marsh and pond at S end of Parque Nacional Queulat, at route 7, leg. R.W. Garrison, 25 i 1995 (RWG); 11 o, seepage 4.5 km E of Puerto Cisnes, leg. R.W. Garrison, 24 i 1995 (RWG); 4 or, stream and seepage 20 km E of Puerto Cisnes, leg. R.W. Garrison, 24 i 1995 (RWG); 1 σ , 1 ϱ , ponds and marsh about 5 km E of La Tapera, leg. R.W. Garrison, 27 i 1995 (RWG); Coihaique Prov., 1 Q, stream in forest 6 km W of Puerto Ramirez, leg. J. Muzón, 24 i 1988 (MLP); 1 of, Puerto Ramirez, pond at Río Futaleufu, leg. J. Muzón, 18 i 1995 (RWG); 1 Q, rivulet and marsh, 5 km W of Puerto Ramirez, by route 231, leg. R.W. Garrison, 18 i 1995 (RWG); Región de Magallanes: Última Esperanza Prov., 1 o, 2 o Parque Nacional Torres del Paine, 11-14 i 2003, leg. A. Vera (NHMS). - Argentina: Neuquén Prov., 1 σ, north shore Lago Lolog, 20 km N San Martin de los Andes, leg. C.M. and O.S. Flint, Jr., 01 i 1994 (RWG).

Maps represent distribution records from collections and reliable references. Maps were created electronically from the Digital Chart of the World (1:1,000,000) using ArcView 8.2. Elevation data and longitude/latitude coordinates were culled from the Global Gazetteer website http://www.fallingrain.com/world/ and placed into a Microsoft FoxPro Data base linked to ArcView.

For the cladistic analysis we used the implicit enumeration command (ie*) in Hennig86 (version 1.5, Farris 1988). According to Theischinger & Watson (1984) and Carle (1995) Gomphomacromia is most closely related to the Australian Archaeophya and Pseudocordulia, and we used these two genera as outgroup taxa, represented by A. magnifica Theischinger & Watson, 1978 and P. circularis Tillyard, 1909. Autapomorphies of terminal taxa were excluded from the analysis. Character matrix and characters are shown in Table 1.

Table 1. Data matrix of diagnostic characters for four ingroup species of *Gomphomacromia* – *G. chilensis* (Gc), *G. fallax* (Gf), *G. nodisticta* (Gn) and *G. paradoxa* (Gp) – and the outgroup taxa *Archaeophya magnifica* (Am) and *Pseudocordulia circularis* (Pc).

Character states	Gc	Gf	Gn	Gp	Am	Pc
Pterothorax lacking mesanepisternal spots (Figs	1a, 2a)					
	•	0	0	0	•	•
Pterothorax with pale mesanepisternal spots (Fig	gs 4a, 5	a, 8a-1	5a)			
	0	•	•	•	0	0
Keel on ♂ tibia I along distal 1/3 - 1/2						
8	•	0	0	•	•	•
Keel on ♂ tibia I along distal 1/2 - 2/3						
0	0	•	•	0	0	0
Ventrolateral edges of of S1 tergum produced into	o dentic	culate p	orojectio	ons (Figs	1e, 3e-	-5e)
	•	0	•	•	•	0
Ventrolateral edges of o S1 tergum smooth (Fig.	2e)					ALCOHOL:
	0	•	0	0	0	•
♂ epiproct triangular						
A PARTY DATE OF THE PARTY OF TH	0	0	0	0	•	•
♂ epiproct quadrangular						
	•	•	•	•	0	0
Q vulvar lamina obsolete or shorter than a third	of SQ					
varvai laitiitta obsolete oi shortei tilait a tilita	0	0	0	0		
Q vulvar lamina projected caudally beyond tip of	USA INCIDENCIAL	District The State of	i 2i 4i	STEEL SHOW AND THE COLUMN	ORGANICATI	
* varvai lainina projected educatily beyond up to	•	(1163 1	., 21, 41		0	0
indicates and management of the control of the cont	Security of the h			Glacilla de Albrida		
Q lobes of vulvar lamina obsolete or very short		_	_	_		
	0	0	0	0		
Q lobes of vulvar lamina long and ca parallel-si	ded (Fig	gs 2i, 5			_	
	0		0		0	0
Q lobes of vulvar lamina long and widening to	tip (Figs	1i, 4i)			_	_
	•	0		0	0	0
Q dorsolateral margin of vulvar lamina entire (Fi	igs 1i, 5	ii)				
	•	0	0	•	•	•
Q dorsolateral margin of vulvar lamina with a tr	iangula	r proje	ction (F	igs 2i, 4	4i)	
	ŏ	•	•	0	0	0
2	allocative collector					
og gonapophyses of S9 very short, tubercle-like	0	^	^	_	TINCHE MINUS	
2 manufactures of SO as large as association 1:		0	0	0		Carl Char
ogonapophyses of S9 as long as cerci (Figs 1i,	21, 41, 5	1)	MARKET THE	energy manufacture	^	^
					0	0
sternum of S10 not projected caudally						
DESIGNATION OF STREET OF STREET	0	0	0	0	•	•
o sternum of S10 prolonged caudally to ca tip of	of cerci	(Figs 1	i, 2i, 4i	, 5i)		
	•	•	•	•	0	0

Gomphomacromia Brauer, 1864 (Figs 1-5, 8-15)

Gomphomacromia paradoxa Brauer, 1864 — type species by monotypy

syn. Cordulia chilensis Hagen, 1861 — nomen nudum

syn. G. paradoxa var. effusa Navás, 1918 — infrasubspecific

syn. G. paradoxa var. tincta Navás, 1918 — infrasubspecific

syn. G. etcheverryi Fraser, 1957 — new synonymy

Gomphomacromia fallax McLachlan, 1881

Gomphomacromia chilensis Martin, 1921

syn. G. mexicana Needham, 1933 — new synonymy

Gomphomacromia nodisticta Ris, 1928

Note: The name "Gomphomacromia fuliginosa Martin, 1921" was introduced in error by Bridges (1994), Steinmann (1997), and Tsuda (2000), since Martin's (1921) record was of Gomphoides fuliginosa.

Gomphomacromia mexicana Needham – a junior synonym of G. chilensis Martin

Needham (1933) compared the holotype male – mentioned as the only dragonfly collected by L.H. Mac Daniels in Teotihuacán during a botanical expedition to Mexico on 26 July 1921 – only with *G. paradoxa* and *G. fallax*, apparently unaware of the description of *G. chilensis*. He diagnosed the species as lacking the yellow antehumeral (= mesanepisternal) spots characteristic of *G. paradoxa* and having dorsum of S9-10 yellow (black in *G. fallax*), which are exactly the same characters used by Martin (1921) for diagnosing his *G. chilensis*. Comparison of structural characters of the holotype male with specimens from Chile identified as *G. chilensis* using Martin's (1921) original description proved them to be conspecific. These include cerci curved down in lateral view (Figs 1c, 3c), ending in rounded tips and convergent in dorsal view (Figs 1d, 3d), shape of distal segment of vesica spermalis, with angulations of distal portion forming acute angles and wider than previous segment, and distal cornu longer than half of distal segment length (Figs 1f, 1g, 3f, 3g), as well as color pattern of thorax and abdomen.

Gomphomacromia etcheverryi Fraser – a junior synonym of G. paradoxa Brauer

Specimens from southern Chile and Argentina usually show narrower (restricted to metepsiternum) and/or divided lateral stripes, than more northern specimens which can have wider (extended over metepisternum and mesepimeron) and/or complete lateral stripes (i.e. Figs 9, 10). However, these differences are not consistent (i.e. Fig. 8 is from a more northern locality than Figs 9, 10), and do not allow separation into two distinct groups, as was well documented by Jurzitza (1981). Jurzitza (1981), perhaps unaware of Fraser's (1957) records of both *G. paradoxa* and *G. etcheverryi* from the same locality (Calafquen, Temuco), considered the two species to be geographically isolated, and assigned northern specimens to *G. etcheverryi* and southern ones to *G. paradoxa*, supported by the following structural characters (states for *G. paradoxa* in parentheses): more flattened cercus tip resul-

ting in a more pronounced dorsal curvature of tip (less flattened and less up-curved), distal cornu of vesica spermalis shorter than half of distal segment and forming a curvature of 45° with the basal portion of the distal segment (as long as half of distal segment and as a linear continuation of the basal portion), distal portion as wide as basal portion of distal segment (distal portion narrower than basal portion), and sides of distal portion forming right angles (sides directed anteriorly).

Although we believe that some of the genitalic characters used by Jurzitza (1981) are useful in diagnosing various *Gomphomacromia* species, we found no differences between northern and southern groups among specimens of *G. paradoxa* and *G. etcheverryi*, nor segregation of specimens into two groups regardless of distribution, based on the combination of characters he provided. For example, there are specimens from southern Chile (i.e. Figs 14b, 15b) with cercus tips as flat as those from some specimens from northern Chile (i.e. Fig. 10), and the length of the distal cornu and the width and angulation of the distal portion of vesica spermalis are variable (i.e. no difference between Figs 9c and 13c, or 11c and 15c, or 8d, 27d and 13d).

More northerly populations include some specimens with wide lateral thoracic markings (extended over mesepimeron, i.e. Figs 9a, 10a), whereas these markings are always restricted to metepisternum in more southerly populations. However, we regard the color differences on which the description of *G. etcheverryi* was based as the result of geographic variability – which was also documented for other groups of dragonflies in the same region, i.e. *Phenes raptor* (Jurzitza 1989) and *Rhionaeschna variegata* (von Ellenrieder 2001), and since we found no characters justifying the separation of two species, we consider *G. etcheverryi* to be a junior synonym of *G. paradoxa*.

Generic diagnosis

Unique for Gomphomacromia are the quadrangular male epiproct (Fig. 4h), vulvar lamina distal half divided into two flap-like rectangular or elliptic lobes (Figs 1i, 2i, 4i, 5i), and female S9 with two caudally directed cylindrical or ribbon-shaped projections, the lateral gonapophyses, approximately as long as cerci and surpassing the posterior margin of S10 (Figs 1i, 2i, 4i, 5i). Species in this genus are small corduliines (35-42 mm), reddish brown to black, lacking metallic reflections, usually with yellow spots or stripes on pterothorax, and paired dorsolateral yellow spots on abdomen. Wings hyaline or with small basal brown or golden nodal spots (Figs 1b-5b); sectors of arculus in Fw separated; supratriangle usually free; subtriangle of Hw usually present (absent in some G. paradoxa); anal loop polygonal, lacking sole and midrib (shared with Lauromacromia). Male tibial keels absent or very short in middle legs, well developed on fore and hind legs; male S7-9 widened. Vulvar lamina projected caudally beyond tip of cerci; female S10 prolonged caudally to about tip of cerci (Figs 1i, 2i, 4i, 5i, shared with Navicordulia).

Species of *Gomphomacromia* can be separated from all New World corduliines by following characters: male auricles with numerous small denticles on inner surface (Fig. 5e); postero-ventral edges of tergum 1 with denticulate projections (Figs 1e, 3e, 4e, 5e, except for *G. fallax*, Fig. 2e); posterior margin of anterior lami-

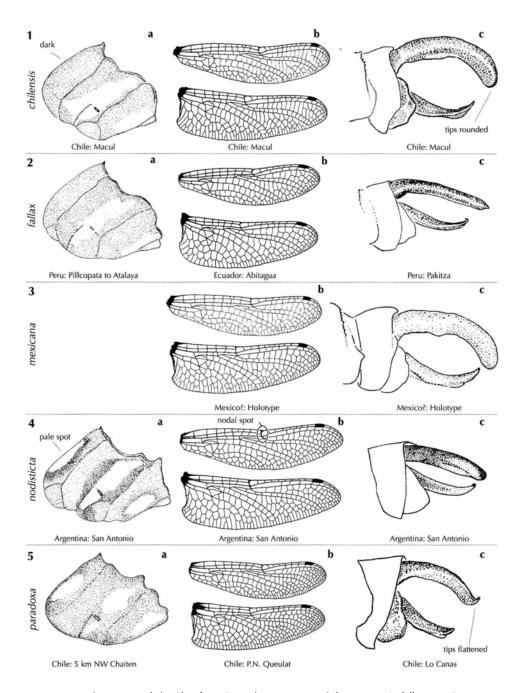
na (Figs 1e-5e) with laminar bilobed lateral projections (possibly fused anterior hamules); genital lobe absent (Fig. 5e); posterior hamule large with a medio-ventral finger-like projection (Figs 1e-5e); distal segment of vesica spermalis with a sclerotized dorso-apical cornu of bifid tip (Figs 1f/g-5f/g, 8c/d-15c/d). All of these characters are shared with the Australian *Archaeophya*; and the laminar projections of the anterior lamina and absence of genital lobe also with *Pseudocordulia*; according to Carle (1995) these three taxa are closely related ('Gomphomacromiidae').

Distribution

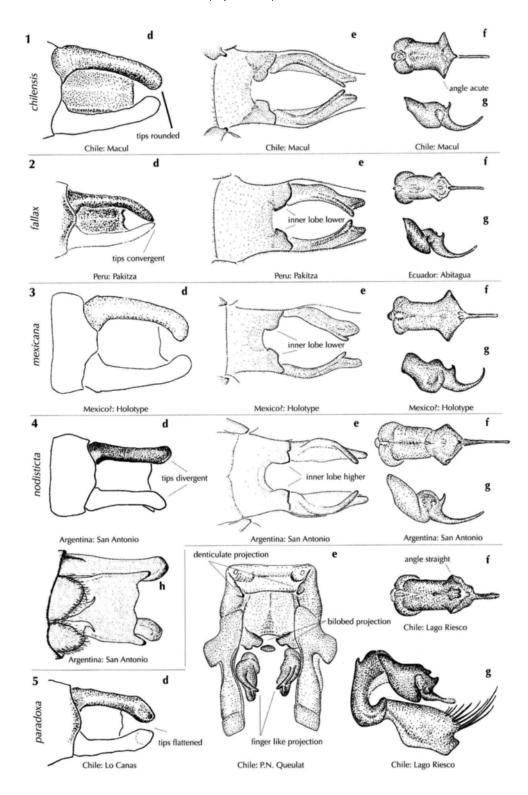
Chile north to Ecuador along the Andes (Figs 6, 7). Old records of the genus from Brazil (i.e. Martin 1907) refer to *Navicordulia*, and Carvalho et al. (2004) recently included *Gomphomacromia* in a key to 'Corduliidae occurring in Brazil' following those records. Fraser's (1947) mention of *G. nodisticta* from Formosa province in Argentina, without providing any precise locality or further data, was probably in error or based on misidentified specimens, since we do not know of any bona fide record of this genus outside of the Andean range. Schmidt's (1942) mention of *G. paradoxa* from Peru was also probably based on a misidentification, since it is well outside the known range of that species. Steinmann (1997) gives 'Chile' as the distribution for *G. nodisticta*, based on an erroneous type locality. The presence of the genus in Mexico is extremely unlikely from a biogeographical standpoint, and the only specimen recorded from Mexico (Teotihuacán), on which the description of *G. mexicana* was based, was most likely mislabeled. We recommend removing those records from the extant distribution lists (i.e. Steinmann 1997; Muzón & von Ellenrieder 1998; Tsuda 2000).

Biology

Found at mountain streams, seepages and bogs. In G. nodisticta and G. paradoxa, males defend small territories from other males, patrolling stream margins or forests paths with a low flight, occasionally perching on stones or low vegetation; mating pairs land on vegetation along stream margins. G. paradoxa is an exception among corduliines in being found in large numbers. At least three of the species of this genus seem to have semi-terrestrial larvae; larvae were found under stones at a distance of ca 3 m from a moist, moss cover rocky area in Osorno province, Chile – unsuccessfully reared in laboratory to know their specific identity, but most likely G. paradoxa based on the locality (N. von Ellenrieder unpubl.) -, and on a moist, moss covered slope on a dirt trail in Pakitza, Peru (Louton et al. 1996; most likely G. fallax). Beckemeyer (2002) reported males of G. fallax in Peru perching alongside narrow roadside trickles beneath cliff sides covered with moss and dripping water, and females flying along the cliff and ovipositing by flicking their abdomens toward the moss. The Australian Pseudocordulia also has seemingly terrestrial larvae (Theischinger & Watson 1984), which would further support their close relationship; the only larva of Gomphomacromia described so far - by supposition based on a specimen without data on habitat found - is that of G. paradoxa (Theischinger & Watson 1984).

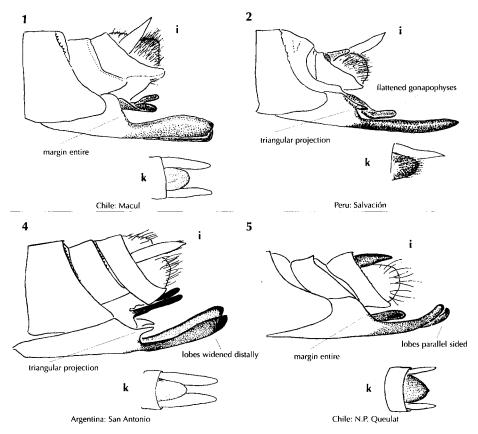


Figures 1-5, a-h: Structural details of (1) Gomphomacromia chilensis, (2) G. fallax, (3) G. mexicana, (4) G. nodisticta, and (5) G. paradoxa — (a) pterothorax, lateral view; (b) wings, lateral view; (c) σ caudal appendages, lateral view; (d) same, dorsal view; (e) σ genital fossa, ventral view; (f) vesica spermalis, distal segment, dorsal view; (g) vesica spermalis, distal segment, lateral view; (5g) entire vesica; (h) ventro-lateral view.



Key to males

1.	Postero-ventral corners of S1 tergum with denticulate projections (Figs 1e, 3e, 4e, 5e); W Argentina along the Andes and Chile (Fig. 6)
1'.	Postero-ventral corners of S1 tergum rounded (Fig. 2e); Yungas (mountain forest) from Ecuador S to Bolivia (Fig. 6)
2.	Cerci tips in dorsal view convergent (Figs 1d, 3d, 5d); inner lobe of anterior lamina posterior process lower than outer lobe (Figs 1e, 3e, 5e); wings hyaline at nodus (Figs 1b, 3b, 5b); Chile and S Argentina (Figs 6, 7)
2'.	Cerci tips in dorsal view divergent (Fig. 4d); inner lobe of anterior lamina posterior process higher than outer lobe (Fig. 4e); wings with nodal yellow spots (Fig. 4b); NW Argentina (Fig. 6)
3.	Cerci in lateral view with rounded tips (Figs 1c, 3c); distal cornu of vesica spermalis about as long as distal segment (Figs 1g, 3g); distal portion of distal segment wider than previous segment and with acute lateral edges (Figs 1f, 3f); mesanepisternum dark (Fig. 1a)
3'.	Cerci in lateral view with depressed tips (Figs 5c/d, 8b-15b); distal cornu of vesica spermalis about as long as half of distal segment (Figs 5g, 8d-15d); distal portion of distal segment about as wide as previous segment and with right angled lateral edges (Figs 5f, 8c-15c); mesanepisternum with paired yellow spots (Figs 5a, 8a-15a)
Ke	y to females
1.	Vulvar lamina with a triangular projection on latero-dorsal margin at level of split of lobes (Figs 2i, 4i); Ecuador south to NW Argentina (Fig. 6)
1'.	Vulvar lamina latero-dorsal margin at level of split of lobes entire (Figs 1i-5i); Chile and S Argentina (Fig. 6)
2.	Gonapophyses of S9 flattened, lobes of vulvar lamina parallel sided (Fig. 2i); wings hyaline at nodus (Fig. 2b); Yungas (mountain forest) from Ecuador S to Bolivia (Fig. 6)
2'.	Gonapophyses of S9 cylindrical, lobes of vulvar lamina widened distally (Fig. 4i); wings with nodal yellow spots (Fig. 4b); NW Argentina (Fig. 6)
	OT NOWSWEW
3.	Lobes of vulvar lamina widened distally (Fig. 1i); epiproct about as long as half of cercus length (Fig. 1k); mesanepisternum dark (Fig. 1a)
3'.	Lobes of vulvar lamina parallel sided (Fig. 5i); epiproct about as long as three fourths of cercus length (Fig. 5k); mesanepisternum with paired yellow spots (Figs 5a, 8a-15a)



Figures 1, 2, 4, 5 - i, k: Structural details of female (1) *Gomphomacromia chilensis*, (2) *G. fallax*, (4) *G. nodisticta*, and (5) *G. paradoxa* — (i) abdominal tip, S8-10, lateral view; (k) abdominal tip, S10, dorsal view.

Cladistic analysis

Following Carle (1995) we have used the Australian genera Archaeophya and Pseudocordulia as outgroup taxa, with which Gomphomacromia shares, besides of the adult characters mentioned under the generic diagnosis, the following larval characters according to Carle (1995): labial palpae without setae along medial margin, lateral prothoracic lobes shelflike, metasternum with transverse sulci fused at short seam, and characters from the proventricular teeth.

Our analysis resulted in one most parsimonious tree (length 12, CI 83, RI 81; Fig. 6), in which G. chilensis is depicted as the sistergroup of the remaining Gomphomacromia species. G. paradoxa, G. nodisticta and G. fallax share the presence of pale mesanepisternal spots, and G. nodisticta and G. fallax form a sistergroup defined by the longer male protibial keels (along distal 1/2-2/3) and the presence of a triangular projection on the dorso-lateral margin of female vulvar lamina. Speciation events in this genus of Gondwanian origin were likely triggered by the Andean orogenesis (Fig. 6).

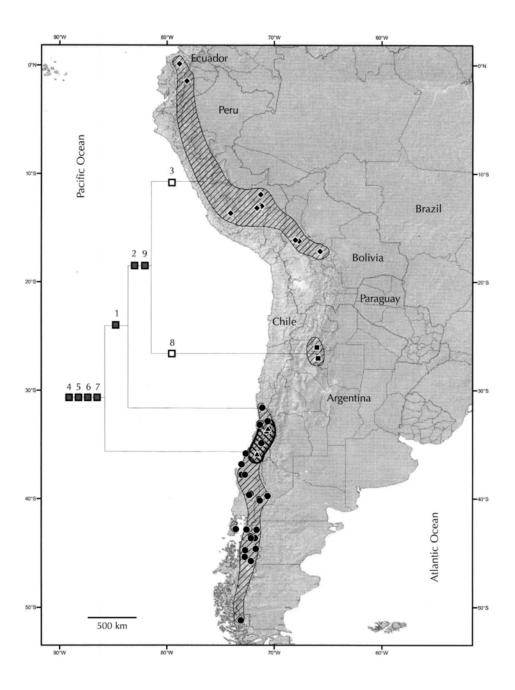


Figure 6: Distribution area and cladogram [length 12, Cl 83, Rl 81] of *Gomphomacromia* spp. — ▲: *G. chilensis*; ♦: *G. fallax*; ■: *G. nodisticta*; ●: *G. paradoxa*; □: Homoplasy; ■: Homology.

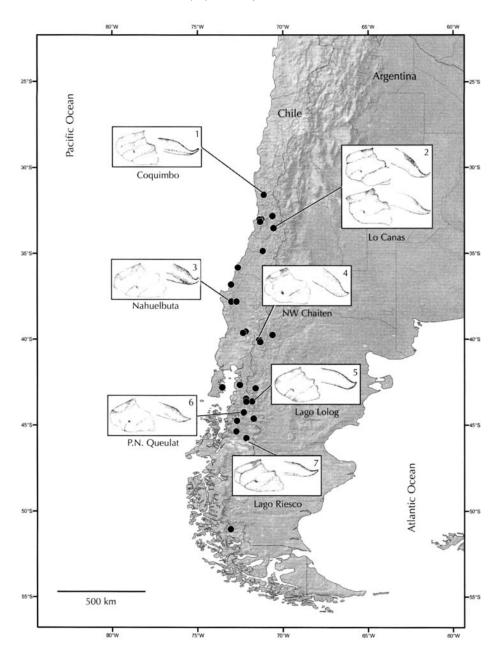
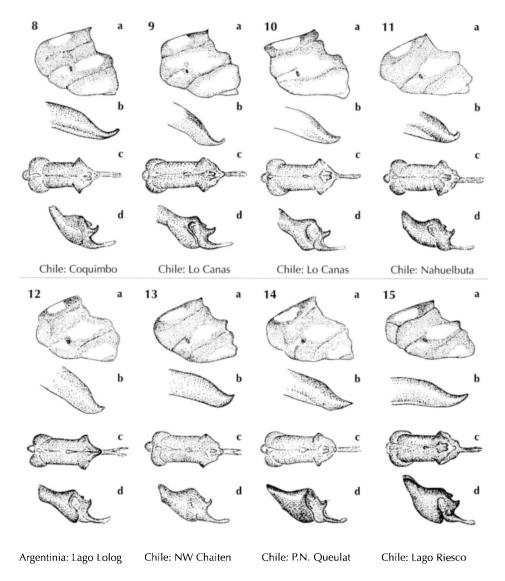


Figure 7: Gomphomacromia paradoxa — distribution area, showing lack of correlation of geography with thoracic color pattern and cercal morphology.



Figures 8-15: Variability in eight specimens of *Gomphomacromia paradoxa* — (a) pterothorax, lateral view; (b) cercus tip, lateral view; (c) vesica spermalis distal segment, dorsal view; (d) vesica spermalis distal segment, lateral view.

ACKNOWLEDGEMENTS

We thank Richard Hoebeke (Cornell University, Ithaca, New York, USA) for the loan of the type of *G. mexicana*, and Javier Muzón (La Plata, Buenos Aires, Argentina), Enrique González Soriano (México City, México), Günther Theischinger (New South Gales, Australia), Jan van Tol (Leiden, The Netherlands), and Wolfgang Schneider (Darmstadt, Germany) for the critical reading of the manuscript.

REFERENCES

- Beckemeyer, R., 2002. Dragonflies in the land of the Incas. Argia 13 (4): 9-11.
- Bridges, C.A., 1994. Catalogue of the family-group, genus-group and species-group names of the Odonata of the world (3rd edition). Bridges, Urbana.
- Carle, F.L., 1995. Evolution, taxonomy and biogeography of ancient Gondwanian libelluloides, with comments on anisopteroid evolution and phylogenetic systematics (Anisoptera: Libelluloidea). Odonatologica 24: 383-424.
- Carvalho, A.L., L.G.V. Salgado & P.C. Werneck-de-Carvalho, 2004. Description of a new species of *Lauromacromia* Geijskes, 1970 (Odonata: Corduliidae) from Southeastern Brazil. Zootaxa 666: 1-11.
- Farris, J.S., 1988. Hennig86, Version 1.5. Farris, Port Jefferson.
- Fraser, F.C., 1947. The Odonata of the Argentine Republic. I. Acta Zoologica Lilloana 4: 427-461.
- Fraser, F.C., 1957. A revision of the Odonata of Chile. Revista Universitaria, Universidad Católica de Chile 42: 153-166.
- Fraser, F.C., 1958. A new species of *Gomphomacromia* (Odon., Gomphidae) from Chile. Entomological Monthly Magazine 94: 53-54.
- González Soriano, E. & R. Novelo Gutiérrez, 1996. Odonata. In: Llorente Bousquets, J.E., A.N. García Aldrete & E. González Soriano (eds) "Biodiversidad, taxonomía y biogeografía de artrópodos de México: Hacia una síntesis de su conocimiento", Universidad Autónoma de México, México D.F., pp. 147-167.
- Jurzitza, G., 1981. Identificación de los representantes chilenos del género *Gomphomacromia* (Corduliidae: Odonata). Revista Chilena de Entomología 11: 31-36.
- Jurzitza, G., 1989. *Phenes raptor centralis* n. subsp. aus Chile (Odonata: Petaluridae). Entomologische Zeitschrift 99: 161-168.
- Louton, J.A., R.W. Garrison & O.S. Flint, 1996. The Odonata of Parque Nacional Manu, Madre de Dios, Peru: natural history, species richness and comparisons with other Peruvian sites. In: Wilson, D.E. & A. Sandoval (eds) "Manu, the biodiversity of southeastern Peru", Smithsonian Institution, Washington D.C., pp. 431-449.
- Martin, R., 1907. Cordulines. Collections Zoologiques du Baron Edm. de Selys Longchamps. Catalogue Systématique et Descriptif 17: 1-94, pls I-III.
- Martin, R., 1921. Sur les Odonates du Chili. Revista Chilena de Historia Natural 25: 19-25. Muzón, J., 1995. Los Odonata de la Patagonia argentina. Revista de la Sociedad Entomológica Argentina 54: 1-14.
- Muzón, J., 1997. Odonata from Patagonia: species richness and distributional patterns. Biogeographica 73: 123-133.
- Muzón, J. & N. von Ellenrieder, 1998. Odonata. In: Morrone, J.J. & S. Coscarón (eds) "Biodiversidad de Artrópodos argentinos. Una perspectiva biotaxonómica", Ediciones Sur, La Plata, pp. 14-21.
- Needham, J.G., 1933. A corduline dragonfly from Mexico (Odonata). Entomological News 44: 88-90.
- Ris, F., 1918. Libellen (Odonaten) aus der Region der amerikanischen Kordilleren von Costa Rica bis Catamarca. Archiv für Naturgeschichte 82 (9): 1-197.
- Ris, F., 1928. Zwei neue Odonaten aus Chile und der Argentinischen Kordillere. Entomologische Mitteilungen 17: 162-174.

- Schmidt, E., 1942. Odonata nebst Bemerkungen über die Anomisma und Chalcopteryx des Amazonas-Gebiets. In: Titschack, E. (ed.) "Beiträge zur Fauna Perus nach der Ausbeute der Hamburger Südperu Expedition 1936, anderer Sammlungen, wie auch auf Grund von Literaturangaben. Band 2", G. Fischer, Jena, pp. 225-276.
- Steinmann, H., 1997. World catalogue of Odonata, vol. 2: Anisoptera. In: Wermuth, H. & M. Fischer (eds) "Das Tierreich. Teilband 111", De Gruyter, Berlin & New York.
- Theischinger, G. & J.A.L. Watson, 1978. The Australian Gomphomacromiinae (Odonata: Corduliidae). Australian Journal of Zoology 26: 399-431.
- Theischinger, G. & J.A.L. Watson, 1984. Larvae of Australian Gomphomacromiinae, and their bearing on the status of the *Synthemis* group of genera (Odonata: Corduliidae). Australian Journal of Zoology 32: 67-95.
- Tsuda, S., 2000. A distributional list of world Odonata 2000. Tsuda, Osaka.
- von Ellenrieder, N., 2000. Additions to the description of *Gomphomacromia nodisticta* Ris, 1928 (Anisoptera: Corduliidae). Bulletin of American Odonatology 6: 7-11.
- von Ellenrieder, N., 2001. A synopsis of the Patagonian species of the genus *Aeshna* Fabricius (Anisoptera: Aeshnidae). Odonatologica 30: 299-325.